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CYTOTAXONOMIC INVESTIGATIONS IN THE *PANICUM MAXIMUM* JACQ. COMPLEX*

I. MORPHOLOGICAL STUDIES

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ABSTRACT

On the basis of morphological characters, twenty indigenous and exotic collections of *Panicum maximum* Jacq. have been classified into five broad types. Morphology (including detailed floral morphology) of these types is described with illustrations. A considerable range of variation of taxonomic significance was met with in them in respect of several characters, both vegetative and floral. Some new characters of diagnostic value, which do not seem to have been reported upon for this species earlier, are described and a handy key to their identification given.

The seed progenies of these morphologically-distinct types were matromorphic and hence exhibited remarkable uniformity within themselves, indicating that the species is highly apomictic.

Some of these types exhibited characters which are considered to be relatively primitive; these characters are described and their phylogenetic significance indicated. Some evolutionary trends in this complex, heterogeneous taxon are discussed.

INTRODUCTION

Guinea grass (*Panicum maximum* Jacq.) is one of the oldest among the introduced grasses in India (Whyte, 1957). It is a valuable fodder grass and is cultivated on a fairly wide scale under irrigated conditions. This species constitutes a heterogeneous assemblage and is poorly understood taxonomically and phylogenetically. Among the different collections of this grass there is considerable variation which is of interest from a taxonomic standpoint. During the course of cytotaxonomic investigations in this taxon, detailed studies on morphological characters, epidermal patterns, cytological and palynological features were undertaken with a view to assessing the precise taxonomic status of the distinct types constituting this species. In the present paper observations on morphological characters are reported. In addition to the characters recorded for this species in the literature, a number of new characters of diagnostic value were discovered and are described below:

MATERIAL AND METHODS

Twenty collections of guinea grass were obtained from different parts of the country and from abroad (Table I). These were grown in the field in a randomized block design with four replications and detailed observations on qualitative and quantitative characters were recorded (Tables IIa, IIb); for this purpose five plants were marked out at random per replication. The colours and their grades with regard to nodal and internodal pigmentation were noted with reference to standard coloured charts of Ridgway (1912). The degree of frost resistance was measured in terms of mean percentage of the foliage that remained green when the plants were exposed to a severe natural incidence of frost during the winter of 1961 when the minimum temperature almost touched 0°C.

OBSERVATIONS

The species *Panicum maximum* has been variously described by different taxonomists including Hooker (1897), Blatter and McCann (1935), Warmke (1951), Meredith (1955), Andrews (1956) and Bor (1960). The twenty collections of the species available for the present investigation were studied (for details, *see* Jauhar, 1963) critically with regard to external morphology (including floral morphology). The collections exhibited interesting differences among themselves with regard to a large number of morphological characters, e.g. growth habit, hairiness and pigmentation of the plant body, panicle and spikelet characters which are normally regarded as being of taxonomic value (Tables IIa and IIb). Morphologically, the twenty collections (serially numbered from 1 to 20 in Table I) broadly fall under the following distinct types:

Type 1: Includes collection Nos. 1 and 17, which are glabrous, macrophyllous, somewhat glaucous and shy-blooming (Plate I, fig. 1)—

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TABLE I

Particulars of the collections of *Panicum maximum* used for the current investigation

Collection No.	Accession No.	Collector	Location
1	EC 2556	Plant Introduction Division, I.A.R.I., New Delhi.	Brazil
2	EC 9721	-do-	Australia
3	EC 7479	H.B. Singh	Australia
4	—	Botany Division	Poona (India)
5	EC 15941	Plant Introduction Division	Australia
6	A 3125	Agronomy Division	U.S.A.
7	—	P. P. Jauhar	Meerut (India)
8	—	P. P. Jauhar	Kanpur (India)
9	—	Agronomy Division	Ajmer (India)
10	A 2341	Agronomy Division	Australia
11	EC 2558	Plant Introduction Division	Brazil
12	A 2342	Agronomy Division	Australia
13	—	P. P. Jauhar	Kanpur (India)
14	—	Agronomy Division	Assam (India)
15	—	P. P. Jauhar	Kota (India)
16	EC 15990	Plant Introduction Division	Australia
17	I.C. 8298	Direct correspondence by the senior author (P. P. J.)	Haringhata, W. Bengal (India)
18	I.C. 8300		,,
19	I.C. 8299		,,
20	I.C. 8407		Poona (India)

TABLE IIa

Distinctive morphological features of the different types of *Panicum maximum*—(i) vegetative characters and degree of frost resistance

Character	Type 1	Type 2	Type 3	Type 4	Type 5	Critical Difference (P=0.05)
Growth habit	Erect open	Erect bushy	Rosette type	Erect open	Erect bushy	•
Degree of branching (Percentage of tillers showing branching)	Absent	50	10	Absent	30	
Culm height (cm)	182.9	150.7	243.4	275.2	186.7	10.0
Number of internodes	9.7	8.9	7.6	10.1	6.5	0.7
Length of second internode (cm)	24.4	16.0	23.8	24.9	21.8	1.6
Thickness of second internode (mm)	4.1	2.5	3.8	4.1	3.4	0.7
Grades of nodal fuzziness	+++	+	++++	++++	++	
Internodal hairiness	—	+	—	+	+++	
Nodal and internodal Pigmentation	—	Maroon or Victoria lake	—	Light Hortense violet	Ox-blood red	
Length of second leaf (cm)	55.7	22.0	30.7	52.9	36.3	5.4
Width of second leaf (cm)	2.6	1.2	1.9	2.4	1.3	0.3
Length of ligule (mm)	2.2	1.7	2.5	2.2	2.6	0.6
Leaf hairiness	—	++++	—	++	+++++	
Leaf-sheath hairiness	—	+++	—	+++	+++++	
Nature of hair	—	Hirtellous (minute, soft)	—	Hispid (long, rough)	Tomentose (long, soft, woolly)	
Leaf margin serration	++	—	++	++	—	
Leaf margin colour	—	—	—	Light pink	Deep maroon	
Frost resistance (Percentage of foliage that remains green during frost)	7.5	50.1	3.6	14.0	17.6	5.5

Note: Grades of nodal fuzziness, leaf and leaf-sheath hairiness and leaf margin serration have been shown in terms of number of + signs; – indicates absence.

TABLE IIb

Distinctive morphological features of the different types of *Panicum maximum*— (ii) floral characters

Character	Type 1	Type 2	Type 3	Type 4	Type 5	Critical Difference (P=0.05)
Days to flowering	135	75	102	115	92	
Length of panicle (cm)	37.5	25.4	40.2	45.6	28.4	2.2
Number of branches	42.6	25.7	36.2	62.2	30.3	1.4
Maximum length of secondary (cm)	20.8	13.3	26.4	22.0	16.4	5.1
Length of spikelet (mm)	3.62	3.57	3.83	3.72	3.86	0.06
Degree of spikelet pubescence	Absent	Densely puberulent	Absent	Absent	Absent	
Spikelet bristles	Absent	Absent	2-4 bristles	Absent	Absent	
Serrations on lower glume	++	+	++	++	++	
Veins of upper glume	5	5	7+1 to 2	5	7+1 to 2	
Veins on lower lemma	5	5	7+1 to 2	5	7	
Serrations on lower palea	—	+++	+++	+	+++ (long and forked)	
Number and size of dentations on upper palea	4 (small)	—	3 (small)	—	7 (long)	

Note: Degree of serrations on lower glume and lower palea is shown in terms of number of + signs; one + sign indicates approximately 5 dents.

flowering only once in two or three years. They exhibit erect-open type of growth habit.

Type 2: Ten collections (Nos. 2, 3, 5, 7, 8, 10, 12, 15, 16 and 20) fall under this type exhibiting almost erect-bushy growth habit. The culms are thin and profusely branched at the upper nodes and the leaves are narrow. The entire plant body, including the spikelets, is finely and densely pubescent; flowering abundantly.

Type 3: Comprises only one collection—No. 4 which has the typical rosette-type of growth habit. A few central tillers grow very tall and bear long widely-spread lax panicles. The spikelets are subtended by bristles, which character is not typical of the genus *Panicum.*

Type 4: Comprises four collections, Nos. 6, 9, 11 and 13. The plants grow very tall, flower abundantly and possess thick culms with prominent nodes and long, broad leaves. Nodes and leaf-sheaths are densely and roughly pubescent.

Type 5: Includes only one collection (No. 14) which is densely hirsute—only the vegetative parts, and not the spikelets, are densely covered with long, woolly hairs. Nodes, internodes, leaves and panicles are deep maroon in colour.

Two collections (Nos. 17 and 19), the samples of which were received under the varietal names, *gongylodes* and *janganika,* resemble each other very closely and they also resemble the thick guinea collections belonging to type 4 above, but they are rather shy-blooming and their leaves are somewhat glabrescent.

Morphological description of the types and additional diagnostic characters:

The five types listed above are remarkably uniform within themselves and strikingly and consistently different from one another in respect of several morphological characters of taxonomic value. Observations recorded on the taxonomic differences of these types are summarised in the Tables IIa and IIb for vegetative and floral characters respectively. Their form of panicle, spikelet and constituent parts of the spikelet are illustrated in Plates I-V. Only some of the major differences are indicated in the tables referred to above. Full morphological description of the five types is given below. For comparison, the relevant descriptions made by earlier authors have been mentioned within brackets:

Type 1: (Plate I, figs. 1-10)
A thick, moderately tillering, non-branching, glabrous, macrophyllous and shy-blooming type (densely tufted, Blatter and McCann, 1935, Andrews, 1956) with erect open type of growth habit (Fig. 1); shoot flattened at the base. *Culms* 170-200 cm tall, 7-11 noded (3-4 noded, Blatter and McCann, 1935, Andrews, 1956); nodes prominent with conspicuous nodal fuzziness; internodes light Viridine green to Baryta yellow in colour, grooved on alternate sides, lower internodes covered with whitish, waxy powder; second internode 20-28 cm long and 3.8-4.2 mm in diameter. *Leaves* thick, coriaceous, glabrous and somewhat glaucous, broad-based, mid-rib prominent, margins serrate; second leaf 50-65 cm long

and 2.3-2.8 cm broad (leaves 25.4-50.8 cm long and 1.3-2.6 cm broad, Blatter and McCann, 1935; 12.7-50.8 cm long and 0.4-2.5 cm broad, Andrews, 1956); leaf-sheaths glaucous and non-hairy, almost completely covering the internodes with one end overlapping the other, margins crimson coloured. *Ligule* (Fig. 2) 2.1-2.4 mm long, membranous, ciliate, with dense hairs behind it.

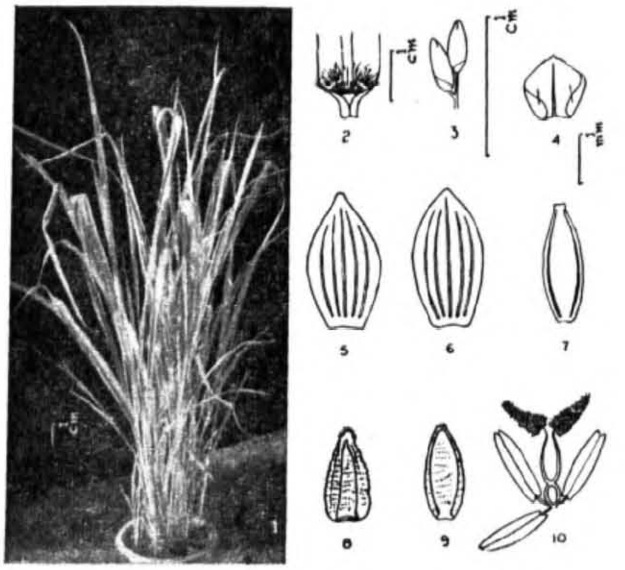

PLATE I

Figs. 1-10 showing a plant, form of ligule, spikelets and constituent parts of the spikelet in *Panicum maximum* Jacq. (Type 1).

1. A fully grown plant bearing no flowers. 2. A portion of leaf showing ligule. *Note* long, dense hairs behind the ligule. 3. A pair of spikelets. 4. Lower glume showing. 3 nerves and serrulated apex. 5. Upper glume 5 nerved. 6. Lower lemma, 5 nerved. 7. Lower palea. 8. Upper lemma conspicuously rugose and 3 nerved. 9. Upper palea showing feeble rugosis. 10. Pistil and stamens.

Note: Figs. 4-10 are to the same scale. Stamens of the staminate floret have not been shown.

Panicle 35-40 cm long (10 to over 45 cm long, Blatter and McCann, 1935; 12-40 cm rarely more, Meredith, 1955; 12.7-38.1 cm or more, Andrews, 1956), lax and highly branched; 35-50 branches in a panicle, branches filiform, length of the longest branch 18-25 cm, lower insertion points of primary branches somewhat hairy. *Spikelets* (Fig. 3) 3.4-3.7 mm long, sub-acute, ovate-oblong, glabrous, sea-green in colour, nerves on glumes and lemmas not prominent; *lower glume* (Fig. 4) upto 1.3 mm long, 3 nerved (3-1 nerved or almost nerveless, Blatter and McCann, 1935; 1-3 nerved or nerveless, Meredith, 1955), margins thin hyaline, involute, apex serrulated; *upper glume* (Fig. 5) almost corresponding in length with the spikelet, sub-acutely to acuminately pointed, 5 nerved, rarely 1 or 2 additional, conspicuous nerves present; *lower lemma* (Fig. 6) 5 nerved, rarely 1 or 2 additional, inconspicuous nerves also present (7 nerved, Blatter and McCann, 1935; 5-7 nerved, Meredith, 1955); *lower palea* (Fig. 7) slightly shorter than the lower lemma, almost oblong, tapering towards the apex which is somewhat cupular; *upper lemma* (Fig. 8) tough, crustaceous, finely rugose, apical portions finely spinulose, 1-3 nerved, nerves being inconspicuous; *upper palea* (Fig. 9) also transversely rugulose; *stigma* tyrian rose; *anthers* (Fig. 10) 1.3-1.6 mm long (1.0-1.5 mm long, Blatter and McCann, 1935).

The above description of Type 1 deviates from the description of *P. maximum* given in the literature (Hooker, 1897; Blatter and McCann, 1935; Andrews, 1956 and Bor, 1960). The following are some of the important, additional characters of diagnostic value:

Lower glume with serrulated apex; *lower-palea* with cupular apex; *upper lemma* 1-3 nerved and with spinulose apex; *upper palea* also transversely rugulose.

Type 2: (Plate II, figs. 1-10)

A thin, highly tillering and profusely branching (sparingly branched, Blatter and McCann, 1935), densely tufted, finely and densely pubescent grass (Fig. 1b) with erect-bushy type of growth habit. *Culms* thin, 135-165 cm tall, sub-erect to geniculate-ascending, 7-10 noded, sometimes rooting from the lower nodes; lower nodes, internodes and margins of leaf-sheaths coloured with pansy-purple pigmentation; upper portions of internodes sparsely pubescent; second internode 12-18 cm long and 2.2-2.8 mm in diameter; nodes prominent and almost glabrous. *Leaves* thin and narrow, hirtellous on both the sides, more or less linear-lanceolate with narrow, contracted base (Fig. 2), margins smooth and mid-rib inconspicuous; second leaf 15-26 cm long and 0.8-1.5 cm broad; leaf-sheaths densely covered with fine, soft, tubercle-based hairs. *Ligule* (Fig. 2) 1.5-1.7 mm long, ciliolate, with dense hairs behind it.

Panicle (Fig. 1) semi-effuse, 20-30 cm long and 10-16 cm broad, scantily branched, spikelets closely spaced or somewhat crowded on the branchlets. *Spikelets* (Fig. 3) puberulent, 3.4-3.6 mm long acute, light parrot-green in colour tinged with purple to maroon pigment; *lower glume* (Fig. 4) 3 nerved with finely serrulated apex; *upper glume* (Fig. 5), like the *lower lemma* (Fig. 6), 5 nerved, unicellular hairs distributed on the glumes and lower lemma. *Lower palea* (Fig. 7) almost oblong, slightly tapering towards the apex which is retuse, margins serrulated; upper floret bisexual and plano-convex in shape; *upper lemma* (Fig. 8) acute, transversely rugose, inconspicuously 3 nerved; *upper palea* (Fig. 9) rugulose; *anthers* (Fig. 10) 1.2-1.4 mm long.

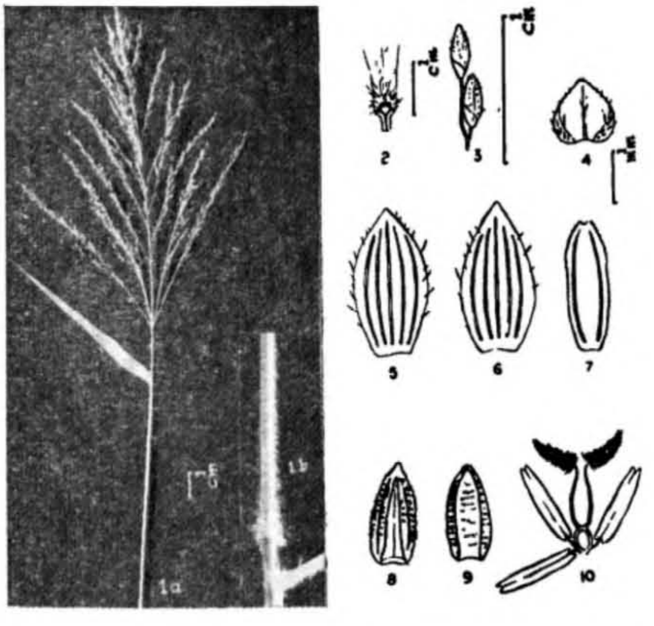

PLATE II

Figs. 1-10 showing form of panicle, ligule, spikelets and constituent parts of a spikelet in *Panicum maximum* Jacq. (Type 2).

1a. Panicle, scantily branched. 1b. A portion of culm magnified to show hirtellous leaf, node and internode. 2. A portion of the leaf showing ligule, and dense pubescence. 3. A pair of puberulent spikelets. *Note* the fine hairs all over. 4. Lower glume, feebly 3 nerved showing pubescence. 5. Upper glume with 5 nerves and fine hairs. 6. Lower lemma 5 nerved. 7. Lower palea showing serrulated margins and cupular apex. 8. Upper lemma showing rugosis and 3 nerves. 9. Upper palea. 10. Pistil and stamens.

Note the feebly nerved glumes and lower lemma etc. Figs. 4-10 are to the same scale. Stamens of the staminate floret have not been shown.

Some of the new characters of this type which do not seem to have been reported earlier are:

Spikelets densely puberulent; *lower palea* with serrulate margins and retuse apex; *upper lemma* inconspicuously 3 nerved; *upper palea* rugulose.

Type 3: (Plate III, figs. 1-10)

This type of *P. maximum* is morphologically-distinct from all other collections of guinea obtained for the present investigation. Its spikelets are subtended by bristles which is not a character of the genus *Panicum*. This type seems to be similar to the variety *gramalote* of *P. maximum* described by Warmke (1951) who mentioned the variety as having its spikelets subtended by 1-3 upturned bristles, 2-3 mm long, and described the insertion points of lowest primary branches of inflorescence as being hairy and the lower surfaces of the leaves sparsely hairy or hairless. Apart from stating these characters Warmke did not describe the variety completely. The present description of this type agrees, to a large measure, with regard to the above characters, with the var. *gramalote* of Warmke (1951). Some additional diagnostic characters of the present collection are, however, given below:

A procerus, sparingly branching, glabrous grass with a typical rosette-type of growth habit. *Culms* 230-260 cm tall (50-200 cm, Meredith, 1955), 6-9 noded; nodes tumid with prominent nodal fuzziness: internodes pale Amparo purple, second internode 21-26 cm long and 3.6-4.2 mm in diameter. *Leaves* almost glabrous, broad-based (Fig. 2), lettuce-green in colour, leaf-margins markedly serrate or almost spinulously scabrous; second leaf 28-35 cm long and 1.7-2.2 cm broad, upper-most leaf very short (Fig. 1); leaf-sheaths glabrous clasping about 2/3 of the internodes. *Ligule* (Fig. 2) prominent, 1.5-1.7 mm long, ciliolate, with long dense hair coming from behind it.

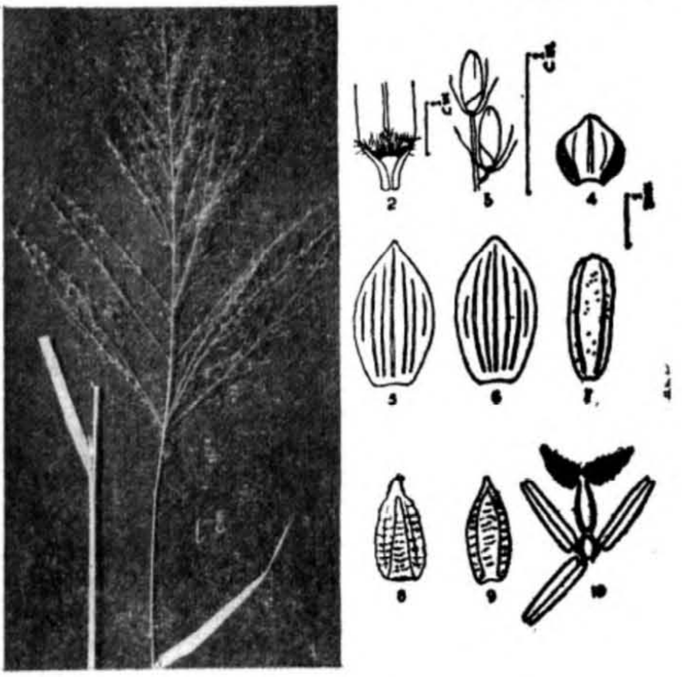

PLATE III

Figs. 1-10 showing form of panicle, flag leaf, ligule, spikelets and constitutent parts of a spikelet in *Panicum maximum* Jacq. (Type 3).

1. A highly spread panicle and a small flag leaf. 2. A portion of leaf showing ligule. *Note* dense hairs behind the ligule. 3. A pair of spikelets subtended by bristles. 4. 3 nerved lower glume. 5. 7 nerved upper glume. 6. 7 nerved lower lemma. 7. Lower palea with serrulated apex. 8. Upper lemma showing conspicuous rugosis, 3 nerves and spinose apex. 9. Finely rugulose upper palea. 10. Pistil and stamens.

Note: Figs. 4-10 are to the same scale. Stamens of the staminate floret have not been shown.

Panicle (Fig. 1) 36-55 cm long and 32-45 cm broad, insertion points of lower primary branches sparsely hairy to hairless (hairy, Warmke, 1951). *Spikelets* (Fig. 3) 3.6-4.0 mm long, glabrous, almost oblong, subtended by 2-4 bristles which are about 3/4 the length of the spikelet; 2-flowered, rarely an additional staminate floret present; *lower glume* (Fig. 4) upto 1.5 mm long, 3 nerved, with notched apex; *upper glume* (Fig. 5) mostly 7 nerved, sometimes 1 or 2 additional inconspicuous nerves also present (5 nerved, Blatter and McCann, 1935; Meredith, 1955); *lower lemma* (Fig. 6) 7-9 nerved; *lower palea* (Fig. 7) almost oblong, 2 nerved, logitudinally rugulose, with serrulose apex; *upper lemma* (Fig. 8) conspicuously rugose, tough, 3-5 nerved, apex spinose to spinulose; *upper palea* (Fig. 9) also somewhat rugulose, semi-crustaceous and almost acuminulately pointed; *stigma* aster-purple; *anthers* (Fig. 10) 1.4-1.8 mm long, orange-chrome when immature, becoming orange-yellow towards maturity.

Type 4: (Plate IV, figs. 1-10)

A thick, robust, tall, highly tillering, sparingly branched to almost unbranched, roughly pubescent, broad-leaved guinea grass with erect open type of growth habit. *Culms* thick, 260-290 cm tall, 8-12 noded; nodes thick with prominent, scaberulous nodal fuzziness, light hortense-violet pigment below the nodes; internodes sparsely hairy on the upper portions, lower internodes being covered with whitish waxy powder; second internode 22-28 cm long and 3.6-4.5 mm thick. *Leaves* thick and somewhat coriaceous, with broad base (Fig. 2), roughly pubescent on the ventral surface, mid-rib prominent, margins serrate; second leaf 40-65 cm long and 2.0-2.7 cm broad; leaf-sheaths densely and roughly pubescent with long, scabrid hairs. *Ligule* (Fig. 2) 1.9-2.4 mm long, ciliate with long, dense, rough hairs behind it.

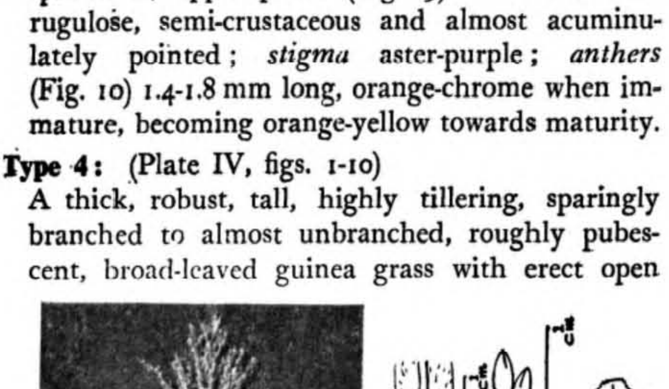

PLATE IV

Figs. 1-10 showing form of panicle, ligule, spikelets and constituent parts of a spikelet in ***Panicum maximum*** **Jacq.** (Type 4).

1. A highly branched panicle. 2. A portion of leaf showing ligule. *Note* long, dense hairs behind the ligule. 3. A pair of spikelets. 4. 3 nerved lower glume with flat and serrulated apex. 5. Upper glume 5 nerved. 6. Lower lemma 5 nerved. 7. Lower palea showing serrulated apical margins. 8. Upper lemma showing rugosis and spinulose apex. 9. Upper palea. 10. Pistil and stamens.

Note : **Figs. 4-10 are to the same scale. Stamens of the staminate floret have not been shown.**

Panicle (Fig. 1) highly effuse and branched, 40-52 cm long and 20-35 cm broad; insertion points of lower primary branches pubescent, spikelets closely spaced or almost crowded on the panicle branchlets. *Spikelets* (Fig. 3) almost ovate-oblong, glabrous, 3.6-3.9 mm long; *lower glume* (Fig. 4) 3 nerved, longitudinally rugulose, apex almost round and notched; *upper glume* (Fig. 5) and *lower lemma* (Fig. 6) 5 nerved; *lower palea* (Fig. 7) hyaline, oblong, longitudinally rugulose with 2 prominent side nerves; *upper lemma* (Fig. 8) tough, crustaceous, rugose, with spinulose apex and 1-3 inconspicuous nerves.

The above description agrees, to some extent, with the one given for *P. maximum* by earlier workers. Some of the additional characters of diagnostic value are, however, described below:

Lower glume and *lower palea* longitudinally rugulose; *upper lemma* with spinulose apex and 1-3 nerves.

Type 5: (Plate V, figs. 1-10)

A medium-thick, moderately tillering and branching, somewhat tufted, brown, tomentose perennial. *Culms* 170-200 cm tall, 5-8 noded. Nodes, internodes, and leaves densely clothed with long, soft, woolly hairs (Fig. 1b) and pigmented with 'Ox-blood-red' colouration; upper internodes Pinnard yellow; second internode 19-25 cm long and 3.0-3.8 mm in diameter. *Leaves* (Fig. 2) almost 'Calla-green' with narrow, contracted base and smooth margins; second leaf 28-42 cm long and 1.4-1.8 cm broad. *Ligule* (Fig. 2) 2.3-3.0 mm long, membranous, ciliate, with long, dense and soft hairs emerging from behind (Fig. 1b).

Panicle (Fig. 1) semi-effuse, deep-maroon in colour, 25-35 cm long and 15-20 cm broad. *Spikelets* (Fig. 3) 3.8-4.0 mm long, glabrous, sub-acute to obtuse or almost oblong; *lower glume* (Fig. 4) 1.3-1.5 mm long, 3-5 nerved (3-1 nerved or almost nerveless, Blatter and McCann, 1935; 1-3 nerved or nerveless, Meredith, 1955), slightly rugulose longitudinally, apex serrulated; *upper glume* (Fig. 5), like the lower lemma (Fig. 6), 7 nerved, longitudinally rugulose, with serrulated, obtuse apex; *lower palea* (Fig. 7) hyaline, almost oblong, prominently serrulated at the upper margins, serrulations sometimes forked; and scattered on the surface. Rarely an additional, small or rudimentary, staminate floret, which has poorly developed lemma and palea and 3 small anthers, present. Upper floret stiff, crustaceous; *upper lemma* (Fig. 8) 3 nerved, conspicuously rugose, with spinose apex, inner margins finely denticulate, side margins strongly ridged; *upper palea* (Fig. 9) semi-crustaceous, rugulose, apex spinulose; *stigma* deep maroon; *anthers* (Fig. 10) upto 2 mm long, deep orange in colour.

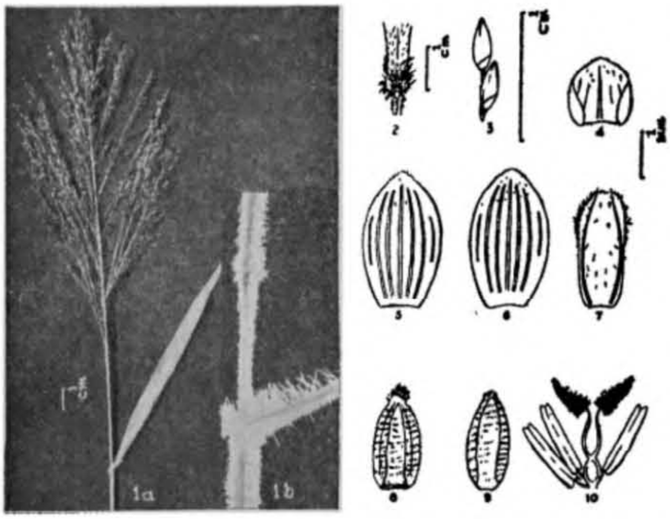

PLATE V

Figs. 1-10 showing form of panicle, ligule, spikelets and constituent parts of the spikelet in *Panicum maximum* Jacq. (Type 5).

1a. Panicle. 1b. A portion of culm magnified to show tomentose leaves, nodes and internodes. 2. A portion of leaf showing ligule. *Note* long, dense hair behind the ligule and all over the leaf. 3. A pair of spikelets. 4. Lower glume showing 5 nerves. 5. Upper glume with 7 nerves. 6. Lower lemma also with 7 nerves. 7. Lower palea showing heavily serrated margins. *Note* long, sometimes forked, serrations. 8. Upper lemma showing conspicuous rugosis, 3 nerves and distinctly spinose apex. 9. Upper palea showing rugosis and spinulose apex. 10. Pistil and stamens.

Note: Multi-nerved glumes and lower lemma, serrulations at the apices of the floral parts and spine-like projections scattered on them. Figs. 4-10 are to the same scale. Stamens of the staminate floret have not been shown.

The above description of Type 5 is quite different from the description given for *P. maximum*. The following are some of the important, additional diagnostic characters for this type:

Tomentose with its nodes, internodes and leaf-sheaths densely clothed with long, soft, woolly hairs and pigmented with 'Ox-blood red' colouration. *Lower glume* 3-5 nerved, somewhat rugulose longitudinally, with serrulated apex. *Upper glume* and the *lower lemma* longitudinally rugulose, with serrulated apex. *Lower palea* prominently serrulated at the upper margins, serrulations being sometimes forked. Rarely an additional, rudimentary staminate floret present. *Upper lemma* 3-nerved, with spinose apex and finely denticulate inner margins and prominently ridged side margins. *Upper palea* semi-crustaceous, rugulose, with spinulose apex; *stigma* deep maroon; *anthers* upto 2 mm long, deep orange in colour.

The two collections (Nos. 17 and 19) received as vars. *gongylodes* and *janganika* respectively, are almost similar to Type 4 above comprising the thick guinea collections. They, however, show a more open type of growth habit; are slightly less densely pubescent, the leaves being somewhat glabrescent; and are more shy-blooming with shorter panicles. Like Type 1, but unlike the collections in Type 4. both the surfaces of leaf blades in these two collections are non-hairy. In all other respects, including spikelet morphology, they are similar to the thick guinea collections included in Type 4.

DISCUSSION

Morphology and Taxonomy

While morphology, including the floral morphology, provides the framework for taxonomy, the morphological characters of the spikelet and inflorescence have special importance in the delineation of taxa in the Gramineae. The shape, texture, hairiness and venation of glumes and lemmas, being rather constant within narrow limits of variation, constitute useful taxonomic features and are often utilized in distinguishing genera and species (Bews, 1929; Church, 1949; Brock and Brown, 1961). Floral characters are undoubtedly more useful to a taxonomist than the vegetative characters (Lawrence, 1951). Some of the vegetative characters are, however, fairly constant and hence of taxonomic value; these include growth habit, form and texture of leaf including leaf base and leaf margins (Lawrence, 1951; Wu, 1962). Leaf-blade and leaf-sheath hairiness, pigmentation and size of plant or leaves are generally useful in the recognition of species or their variants (Percival, 1921; Harrington, 1932; Pal, Ramanujam and Memon, 1952). In the present investigation, apart from studying vegetative characters, such as growth habit, height of plant, leaf size, shape and texture, leaf and leaf-sheath hairiness and pigmentation, relatively greater emphasis has been placed on floral characters—including shape, texture, serration and nervation of each constituent part of the spikelet. The study has provided some very interesting information in that it has been possible to add a number of new diagnostic characters for describing the material under study.

While all the 20 different collections of *Panicum maximum* included in this study show the character, rugosis of the upper lemma (*see* Plates I to V), which is regarded as the typical or key character for this species, they represent a highly heterogeneous group in respect of many other characters of diagnostic value. Morphologically, they constitute five distinct types which are uniform within themselves but are consistently different from one another as though they were distinct subspecies, if not species. A handy key to their identification is given below:

Scheme of classification of Panicum maximum complex

- 1a. Spikelets non-pubescent
- 1b. Spikelets pubescent
  - 2a. Spikelets subtended by bristles
  - 2b. Spikelets not subtended by bristles
    - 3a. Leaf-sheath pubescent
    - 3b. Leaf-sheath non-pubescent
      - 4a. Both surfaces of leaf-blade non-hairy
      - 4b. Upper surface of leaf-blade hairy
      - 4c. Both surfaces of leaf-blade hairy

Key to the types of P. maximum

- 1a. Spikelets non-pubescent
  - 2a. Spikelets subtended by bristles ...*Type* 3
  - 2b. Spikelets not subtended by bristles
    - 3a. Leaf-sheath pubescent
      - 4b. Upper surface of leaf-blade hairy ...*Type* 4
      - 4c. Both surfaces of leaf-blade hairy ...*Type* 5
    - 3b. Leaf-sheath non-pubescent
      - 4a. Both surfaces of leaf-blade non-hairy ...*Type* 1
- 1b. Spikelets pubescent
  - 2b. Spikelets not subtended by bristles
    - 3a. Leaf-sheath pubescent
      - 4c. Both surfaces of leaf-blade hairy ...*Type* 2

Mode of reproduction in *P. maximum*

Numerous inter-type crosses attempted in different combinations by various techniques of emasculation and pollination recommended for this group of plants did not result in the production of any true hybrid. The seed progenies of the different morphologically-distinct 'types' of this grass exhibited remarkable uniformity within themselves and striking differences between themselves with regard to several characters—quantitative as well as qualitative. Some of these differences were evident even at the seedling stage. This uniformity among the seed progenies of the different types, in contrast to the enormous variation in the seed progenies of the diploid sexual species, *P. antidotale* and *P. cymbiforme* (Jauhar, 1966) clearly indicates a highly apomictic mode of reproduction in this grass. The reasonable level of seed setting observed in the different types of *P. maximum* in spite of the extremely irregular meiosis (Jauhar, 1963) would further indicate the high incidence of apomixis in this species.

Warmke (1951) first indicated the existence of apomixis in *P. maximum* and later (Warmke, 1954) he showed the presence of apospory combined with pseudogamy to exist in this species. Brown and Emery (1958) also found this species to be highly aposporous. It is difficult to say as to when apomixis set in within this *P. maximum* complex. This apomictic mode of reproduction appears to have been responsible for preserving numerous characters, including those which could have arisen through mutation.

Evolutionary trends

It is interesting to note that some of the collections of this grass show characters which are regarded as being relatively primitive on the evolutionary scale. For example, as will be seen from Table IIb, Types 1, 3 and 4 have highly branched and spreading panicles. Types 3 and 5 have many-nerved glumes and lemmas and also occasionally have an additional staminate floret in their spikelets. All these characters have been considered to represent primitive conditions within the grass family (Bews, 1929; Hubbard, 1948; and others) and are characteristic of the primitive Bambuseae (Bews, 1929; Lawrence, 1951; Harlan, 1956). Thus the presence of an assemblage of primitive characters in *P. maximum,* a panicoid grass, and also in the Bambuseae, lends support to Harlan's (1956) views regarding the direct derivation of Panicoideae from the bamboos and their allies. Morphological and epidermological studies made on some species of *Panicum* (Jauhar, 1966, 1967) also point to the evolutionary relationship between the Paniceae and the Bambuseae.

Another important feature noticed was the presence of a character not ascribed to the genus *Panicum* (Bor, 1960). Type 3 of *P. maximum* described here has its spikelets subtended by 2-4 bristles. This character does not, therefore, seem to have come from infrageneric limits. It may have had its origin as a major mutation. Alternatively, this character could have introgressed into this species from other genera like *Setaria* or *Pennisetum.* However, the possibility of such a transfer appears to be far-fetched for the following reasons:

(i) In view of the high incidence of apomixis in *P. maximum* such intergeneric hybridization would be extremely difficult. (ii) If such hybridization involved diploid and presumably sexual forms of *P. maximum*, one would have expected some other characters of *Setaria* or *Pennisetum* also to have been transferred, but no other characters of these genera, except the spikelet bristles, are present in Type 3. (iii) Meiosis in *P. maximum* is characterised by the high frequency of quadrivalents, up to 6 IV per P. M. C. (Jauhar, 1963); if the species had some chromatin material from *Setaria* or other genera such a high frequency of multivalent formation could not be expected. It, therefore, appears that this character of bristling in *P. maximum* arose through mutation and has been preserved through apomixis. Similarly, the character of pubescence of spikelets of Type 2 could have arisen through mutation. Thus, mutations appear to have played an important role in the creation of subspecific variation in this agamospecies.

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